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HERBARIUM TAXONOMY VERSUS FIELD KNOWLEDGE

Is there an attainable solution?

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Evolution is a complex process and the species produced by evolutionary processes are therefore of necessity not always clear-cut. Problems associated with definition of species boundaries have always plagued taxonomists and, no doubt, always will. However, I would maintain that in most situations there really is a 'best' solution to what kind of taxonomic recognition to accord a specific evolutionary pattern.

The optimum solution to these kinds of problems depends in part on taxonomic philosophy. Are species real objective evolutionary entities? (Our job being to find out what they are.) Or are they essentially artificial constructs whose delimitation more or less depends on taxonomic convenience and preference? In the latter case, there is no 'solution' to the taxonomists' dilemma. Certainly, many people working in the temperate zone, where rampant autogamy means that every clone of *Taraxacum* is essentially a different microspecies, tend to feel that this is the case. However, many of us working in the Neotropics feel that species are mostly far better defined and are, for the most part, quite objective entities. Indeed, as I see it, if species are not in some sense real units whose nature and limits we are trying to discover via scientific thought processes, taxonomy would hardly be worth doing, and we should turn our efforts to some other field of endeavor, say, population genetics, where the scientific method does provide insight into the real world.

At least in the Neotropics, distinctions between species are, for the most part, rather well-defined, although often by subtle characters. A typical pattern of speciation is vegetative differentiation adapting two closely related taxa of a genus to different substrates, or a switch from wind-dispersal to water-dispersal in a swamp derivative of an upland forest taxon. These patterns are usually very clear in the field, but extremely hard to understand in the herbarium.

If two closely related species fulfill two different evolutionary roles (i.e., occupy different habitats), then philosophically they are clearly worthy of taxonomic recognition. In practice, however, problems arise when a species is looked at over a broader range. The same, or even greater, differences that serve to differentiate a taxon locally may crop up elsewhere in the range of a species in a different evolutionary context. In other words, in some places the same amount of morphological (and presumably genetic) variation may be interpopulational, whereas in others it is clearly separable into distinct taxonomically circumscribable units.

This kind of pattern, the infamous polymorphic species that has been responsible for so many taxonomic headaches, may not have a clearly optimum solution. However, I would suggest the generality that (contrary to my own earlier work) in the lowland continental Neotropics it is usually possible to resolve polymorphic species into satisfyingly discrete entities. On the other hand, in my experience in Africa, the same levels of morphological differentiation tend not to be partitionable into reasonably discrete taxonomically recognizable subunits. I currently recognize far greater morphological variability within most wide-ranging species of African Bignoniaceae than I would be willing to accept within a Neotropical taxon. I have spent an inordinate amount of time trying to make the African taxa fit the Neotropical patterns, but to no avail. It may be that different evolutionary processes on the two continents have led to what we see today. In any event, each such case will certainly have to be resolved on its own merits by the taxonomist involved.

Again – in my own experience, and drawing heavily on Bignoniaceae patterns – Madagascar seems to follow the Neotropical pattern, with mostly quite clear-cut species.

What about Malesia? Can useful generalities about the best resolution of polymorphic species complexes be arrived at? It seems clear that – at least in some groups – for example, the Dipterocarpaceae, rather fine specific delimitation correlated with ecology and microgeography can be worked out. I also know from discussions with colleagues who know the Queensland flora very well that they feel that there are generally discrete ecotaxonomically recognizable entities in their rain forest, which can (and should) be recognized at a far finer level of specific resolution than has been prevalent in recent taxonomy in the Indonesian region. It is most interesting that Professor van Steenis, himself, who also worked with Bignoniaceae, came up with two quite different solutions for the proper taxonomic treatment of Malesian bignons. In his early work, he split them rather finely, but in his recent treatment for the *Flora Malesiana*, he lumps together many of the species that he had earlier described. Does this reflect an 'African' situation, where additional collections fill in the supposed gaps between different entities and make specific delimitation much harder to define? Or does it merely reflect a change in philosophy?

To some degree, there is a solution to this kind of problem. It is the obvious one of gathering a more complete database, both through very many more collections and through much more intensive field study. It is dramatic what a high percentage of our

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knowledge of the Neotropical flora has come in the last decade or so, through greatly intensified programs of field work and general collecting. The conclusions that we now tend to reach about generally clear-cut species, often correlated with local ecology, are very different from the ones that would have been reached a decade or more ago in the absence of all of the collections that are now available. It is significant that from the Malesian region most of the collections are much older and the modern, nearly geometric increase in collecting activity that has characterized the Neotropics seems not to have taken place, or at least has not taken place to the same degree. At the very least, we should be able to make our taxonomy reflect, as nearly as possible, the actual situation in nature, by gathering additional data.

While the above kinds of situations may or may not have optimal taxonomic solutions, there is a second kind of problem which very clearly does, and it is in this situation where it seems very clear to me that the philosophy of taxonomic lumping that has characterized Leiden, the Netherlands, taxonomists in general, and especially much work in the Flora Malesiana, has done a significant disservice to taxonomy. It is in the situation that I am about to describe that the knowledge of the field botanist can and must take preeminence over that of the herbarium-based monographer. This is the case of closely related taxa that co-occur together in exactly the same forest, but *behave* as distinct species. In other words, they 'pass the test of sympatry.'

I first came face to face with this problem while preparing the Flora of Río Palenque, where, in a number of cases, two very distinctive species were identified with the same name by the relevant specialist. In one case, two species of Maquira, a Moraceae, were clearly recognizable, one being a large tree, the other a mid-canopy tree. One had darker latex than the other. One had longer petioles and a slightly differently shaped leaf than the other (although there was some overlap in the leaf character). Perhaps more telling, one of them had strongly pubescent fruits, while the other had glabrous fruits. Very clearly, two species are involved. In another case, one type of Dichorisandra is a vine with two blue petals and one white one, and a rather small, open inflorescence, whereas a second species at Río Palenque is always erect, with a much denser inflorescence and blue flowers. No one looking at these two very different plants in the field would ever consider them to be conspecific. A similar example that has become rather infamous in the Neotropics comes from the La Selva field station in Costa Rica, where six different, locally occurring species of Guarea, well known in the field to many ecologists who had studied their fruiting, were lumped together under Guarea glabra in a recent Flora Neotropica monograph. In each of these cases, the monographer justified his decision by the complexity of the variation patterns elsewhere in the range of a species complex. However, in such cases, it seems very clear to me that no matter how much more difficult it may make a taxonomist's work, it is incumbent on him to recognize taxa that so clearly pass the test of sympatry as species and then work out from that objective starting point, instead of vice versa.

I have also been on the other side of this particular situation. For some years, I have been involved in a debate with Brazilian botanists who claim that I have been lumping too much variability into Tabebuia serratifolia. Specifically, two types of yellow-flowered Tabebuia that grow together at Linhares, in Espirito Santo, are recognized by the local people, but not by me. As in nearly all such cases, there turned out to be a very clear 'right' and 'wrong': when I finally got adequate material to more carefully examine the situation, there turned out to be several very good morphological characters (the best being presence or absence of pubescence in the corolla throat) to distinguish these two entities as species. One further example that illustrates an additional ramification of this type of problem is worth mentioning. Arrabidaea chica and A. candicans grow together sympatrically in southern Central America. Although one of them tends to be in dryer forests than the other, they both grow together in a number of lowland moist forests. The only real differentiating character is that one is densely white pubescent on the leaf undersurface and the other is glabrous. Whereas in southern Central America this rather minor character very clearly distinguishes two different entities, it is possible to discover both leaf types growing on the same individual plant in Belize and in the dry part of western Ecuador. Does this mean that the pubescent and nonpubescent forms should be lumped together? Most emphatically not: not only are they (rather slightly) morphologically differentiated, but these two species flower at completely different times of the year where they grow together in Central America. Moreover, the few individuals that have both glabrous and hairy leaves at the extremes of the species range have only the most juvenile leaves with pubescence approximating that of A. candicans, whereas older leaves are either uniformly more pubescent or uniformly glabrous, just as in Central America. Given the ecological clue of a completely different phenological behavior where the two entities co-occur, I think there would be little disagreement that these should be regarded as specifically distinct.

In this kind of situation I believe that additional collections (including sterile collections which are often much easier to obtain), especially when associated with the ecological data, will resolve the perceived discrepancies between the herbarium taxonomist and the field-based one.

There is yet a third situation, where differences between different taxonomic philosophies might be soluble, but perhaps only if political considerations are included in the decision-making process. This is the case of extremely dynamic evolution in action, for example, what seems to be occurring in cloud forests along the base of the Andes. We think we have seen speciation taking place in situ in nature in as little as 15 years in certain cloud forest orchids. Preliminary evidence suggests that every slightly isolated cloud forest ridgetop may have a large complement of endemic species, most of these very little differentiated from their congeners elsewhere. In the single case where such a situation has been examined genetically, the similarity or dissimilarity of DNA turned

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out to be 'just another character' with two derivative species of *Lisianthus* that had arisen as local endemics on different cloud forest ridges from the same ancestral lowland population being differentiated in one case very clearly by a switch in flower color and shape associated with hummingbird pollination (but no discernable genetic differentiation), whereas in the other locally endemic taxon, hardly differentiable morphologically on account of slightly more coriaceous leaves, there was a dramatic change in the DNA sequence. If genetic relatedness does not provide much of a guideline for the taxonomist to resolve these situations, are we again at the place where the individual taxonomist's gut feel becomes the only practical guideline? Or perhaps the taxonomic community could (and should?) suggest guidelines drawing on the principle that the populations isolated on different ridge tops or equivalents are fulfilling 'unitary evolutionary roles' and should therefore be recognized as species inasmuch as practical.

The easiest solution for a monographer may well be to sweep the variation under the rug and lump problem complexes together (the process that seems to me inevitable in many African taxa, and that I used to follow with Neotropical Bignoniaceae, as well). However, it also behooves us to remember our responsibility in cataloging the world's tropical biodiversity. Variation that is swept under the rug is lost from view, whereas that which is grappled with openly, albeit at great cost of taxonomic time and effort, makes information available to the general public through our taxonomic treatises. In view of the current biodiversity crisis and the necessity of providing floristic (and faunistic) data as a basis for understanding, conserving, and ultimately using this biodiversity, it seems to me that there is a political imperative as well as a scientific one to accord specific recognition to taxa that can be clearly demonstrated to behave, either genetically or ecologically, as species.

Undoubtedly, the 'solution' to the difference in opinion between herbarium taxonomy and field knowledge will only be a partial one. However, it is abundantly clear that the two can be brought much closer together. It seems that the key point might well be to remove the distinction between the herbarium worker and the field worker by converting the former into the latter. Given the current international outcry about the loss of uncataloged biodiversity in the Tropics, this may well become an increasingly viable possibility, if the taxonomic community can find effective ways of impressing upon funding agencies and decision makers the importance of this step if we are to produce the catalogs of biodiversity that they expect from us.